

Different traits predict competitive effect versus response by *Bromus madritensis* in its native and invasive ranges

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ABSTRACT (250 words maximum)

Community assembly and coexistence theories predict that both fitness and plant functional traits should influence competitive interactions between native and invasive species. The evolution of the increased competitive ability (EICA) hypothesis predicts that species will grow larger (a measure of fitness) in their invasive than native range; hence we hypothesized that species might exert greater competitive effects in their invasive range, lessening the importance of functional traits. In a greenhouse experiment we compared traits and competitive interactions between *Bromus madritensis* (an annual grass) and resident species from its native range in Spain, and its invaded range in Southern California. *B. madritensis* collected in California grew larger and had a greater competitive effect on resident species than *B. madritensis* collected in Spain. However, resident species from California also suppressed the growth of *B. madritensis* more than species from its native range in Spain. Competitive interaction strengths were predicted by different suites of traits in the native versus invasive range of *B. madritensis*; surprisingly however, size of the competitor (fitness), did not predict variation in competitive interactions. This study shows that different suites of traits may aid in identifying those native species likely to strongly compete with invaders, versus those that will be competitively suppressed by invaders, with important implications for the design of restoration efforts aiming to promote native species growth and prevent invasion. More generally, our study shows that fitness differences may not be as important as traits when predicting competitive outcomes in this system.

Keywords: coexistence, EICA, fitness differences, functional traits, limiting similarity

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INTRODUCTION

Invasive plants impact ecosystem processes (Liao et al. 2008) and biodiversity, reducing the richness and abundance of native species at local scales (Powell et al. 2011; Vilà et al. 2011). Although the mechanisms that underlie these impacts are increasingly understood (Levine et al. 2003), there is great variation among invader species in how they impact resident communities, with some exotic species having strong effects, and others have little or no impact (Pyšek et al. 2012). Theory in invasion biology often relies on plant functional traits to reflect species' ecological strategies, and indeed invasive species often possess traits that differ from non-invasive or native species (Pyšek and Richardson 2008; Van Kleunen et al. 2010). While there has been a call to evaluate whether traits related to the likelihood of invasion correspond with the impacts of invasive species (MacDougall et al. 2009; Pyšek et al. 2012), few empirical studies on the topic exist.

Theories from community ecology predict that functional traits and measures of plant fitness should influence both the likelihood that a species will invade, and the competitive impact of the invader on resident species. For instance, the theory of limiting similarity posits that species with overlapping niches will compete strongly for resources, such that successful invaders must be functionally dissimilar from residents to succeed (Abrams 1983; MacArthur and Levins 1967; Schilke and Ackerly 2005). Consistent with this theory, plant functional traits often reflect variation in strategies of life-history and resource-capture (Diaz et al. 1998; Lavorel and Garnier 2002), and experimental tests often find that invaders with traits similar to residents have a lower probability of invading than those with traits that differ from residents (Dukes 2002; Emery 2007; Fargione et al. 2003; Von Holle and Simberloff 2004). A recent meta-analysis suggests that while many studies show support for a role of limiting similarity in predicting the likelihood of invader establishment, the performance of established invasive species is not influenced by the traits of residents (Price and Pärtel 2013).

Coexistence theory predicts that a species can invade a new system in the absence of niche differences if the species has higher fitness than resident species (Chesson 2000; MacDougall et al. 2009). Invasive species are often larger or have higher seed set than non-invasive species from their home ranges (Jelbert et al. 2015), suggesting a general competitive advantage. Invaders also often achieve larger sizes in their invading ranges than in their home ranges, a pattern that is also suggestive of a fitness advantage (Crawley 1987; Parker et al. 2013).

The evolution of increased competitive ability hypothesis (EICA) predicts that selection will act upon invading species that have escaped their specialist enemies (Keane and Crawley 2002), resulting in reduced allocation to defense and increased allocation to vegetative growth (Blossey and Notzold 1995). Few studies have explicitly evaluated the relative roles of trait and fitness differences to predict the outcome of competitive interactions between native and invading species. A recent study demonstrated that while some species invade by competitively excluding residents, other invaders may be successful by having traits and relative fitness differences that enable coexistence with resident species (Lai et al. 2015).

Traits may be differentially important for understanding the competitive effect of invaders on residents versus the competitive response of invaders to the resident community (*sensu* Goldberg 1990). Traits related to plant size (fitness), for instance, are thought to relate to the ability to draw down many resources simultaneously, potentially explaining the concordance between competitive hierarchies based on competitive effect versus response (Goldberg and Landa 1991). Leaf traits, such as higher specific leaf area (SLA) that correlate with plant life strategies (Wilson et al. 1999) and high rates of resource capture (Garnier et al. 2001) have also been associated with invader success (Feng et al. 2008; Grotkopp and Rejmánek 2007), although traits associated with high resource-use efficiency predict invasions in some systems (Funk and Vitousek 2007). Fast germination is another trait that has been hypothesized to confer a seasonal priority-advantage to early-active species, and has been found to be associated with non-native species that can competitively suppress later-germinating native species (Wainwright et al. 2012).

Trait-based competitive hierarchies have been described in many systems, from forests to annual-dominated communities (Kraft et al. 2014; Kunstler et al. 2012), but few have focused on the competitive interactions of species in their native and invaded ranges. A key study found that competition from neighbors caused a greater reduction in the growth of *Centaurea strobe* in its native than invasive range, although the mechanism was

not identified (Callaway et al. 2011). If evolved competitive ability contributes to invasion success, and invasion releases exotic species from stabilizing controls like herbivores and diseases, then invading species should exhibit differences in traits between the invaded and native range. Therefore, the relative roles of trait versus fitness differences for predicting competition outcomes may vary between a species in native and invasive ranges.

In this study, we aimed to determine the relative roles of functional traits and fitness differences for predicting the response of an invader to competition with residents and the competitive effect of the invader on residents. To do this, we focused on the invasive species *Bromus madritensis* (common name: compact brome), an annual grass, native to western and southern Europe. *B. madritensis* has become a problematic invader in Southern California and in other Mediterranean systems (e.g. Wainwright et al. 2016) within the last 300 years (Watson 1880). We focus on two populations of *B. madritensis*- one from within its native range (Madrid, Spain – ‘native’) and one from within its invaded range (Southern California-‘invasive’), and evaluated its competitive interactions with resident species from each region. We hypothesized that:

- (i) *B. madritensis* would achieve larger size (a proxy for fitness, Younginger 2017) and have different trait means in its invaded than native range, consistent with the EICA hypothesis, and that as a result,
- (ii) *B. madritensis* would have a lower competitive response to residents in the invaded community than residents in its native community,
- (iii) *B. madritensis* would have a greater competitive effect on residents in the invaded community than residents in its native community, and
- (iv) competitive outcomes would be driven by a combination of fitness and trait differences, but that fitness differences would play a greater role in invader success in the invaded range.

METHODS

Seed collection

Resident competitor species for this experiment are listed in Table 1. Seed collections were collected from one site each in Spain and California, meaning that the experiment compares just two populations of the focal species. In Spain, seeds of *B. madritensis* and the most commonly co-occurring species were collected by Francisco Martín Azcárate in the Spring of 2014, near the municipality of Colmenar Viejo, 30km north of Madrid (approx. 850 m altitude). The site has a granite substrate, and a typical mediterranean climate (13.5°C mean annual temperature, 550 mm mean annual rainfall, severe summer drought). Seeds were collected from as many plants as possible, keeping a distance of at least 10 m between individuals.

In California, seeds of *B. madritensis* and common, co-occurring species were collected from the UC San Diego Ecological Park in May 2015. This time period corresponded with an extreme drought event calculated as having a greater than 10,000 year return interval (Robeson 2015). As a result, there were insufficient seeds collected from other resident species in the community to conduct the planned experiment, so seeds of commonly co-occurring species were purchased from S&S Seeds (Carpenteria, California).

This study focuses on only one location and set of populations in California and Spain, respectively. We acknowledge that using only one population from each location may not be representative of all populations of *B. madritensis*. For instance, high genetic and phenotypic diversity has been found across populations in the invasive range of its congener, *Bromus tectorum* (Huft and Zelikova 2016).

Experimental design

Experiments were conducted in a greenhouse at the University of California, San Diego Biology Field Station in La Jolla, CA, USA. Seeds were planted in cylindrical pots (3.8 cm wide, 18.4 cm deep) containing homogenized local topsoil (Agriservices Inc, Oceanside CA). Seeds from each *B. madritensis* population (Spain and California) were planted both alone and in pairwise competition with resident species from Spain and California (Table 1). Resident species were also grown alone to estimate the competitive effect of *B. madritensis*. Seed planting numbers varied according to pre-estimated germination rates. The seeds of all species were sowed on September 1,

2015. Species did differ in seed germination time thus averaged germination dates for each species were included in the analysis as a trait. Following germination, seedlings were weeded to achieve one seedling per pot (absence of competition) or six seedlings per pot to replicate diffuse competition (interspecific competition, three seedlings of a given competitor species and three *B. madritensis* seedlings from the same source location). While this design includes intraspecific competition between both the target and resident species by its very nature, only interspecific competition was measured. Intraspecific competition cannot be separated from the interspecific competition in this design and so was not included in any analyses. There were eight replicates planted for each treatment. The two *B. madritensis* populations were not planted together in competition, nor were *B. madritensis* from Spain planted with resident species from California (nor vice versa) in this experiment.

Above-ground biomass was harvested after 10 weeks, which corresponds to the time from germination to peak biomass for nearby herbaceous communities in Southern California (Cleland et al. 2016). For individuals grown alone, below-ground biomass was also harvested. Above-ground biomass was clipped at soil level. Below-ground biomass was rinsed from the soil over a 1 mm sieve. All samples were dried to a constant mass at 40°C for 48 hours, and weighed to the nearest 0.01 mg.

Competition Index

Relative Interaction Intensity (RII) was calculated from plants grown in competition treatments according to Equations 1 and 2 (Armas et al. 2004). This metric is bounded between -1, representing extreme competition, and +1, representing strong facilitation.

$$\text{Competitive effect} = \frac{\text{Biomass of resident grown with } B. \text{ madritensis} - \text{biomass of resident grown alone}}{\text{Biomass of resident grown alone} + \text{biomass of resident grown with } B. \text{ madritensis}}$$

(Eq. 1)

$$\text{Competitive response} = \frac{\text{Biomass of } B. \text{ madritensis grown with resident} - \text{Biomass of } B. \text{ madritensis grown alone}}{\text{Biomass of } B. \text{ madritensis grown alone} + \text{Biomass of } B. \text{ madritensis grown with resident}}$$

(Eq. 2)

Traits

Plant functional traits were measured for the invader and resident species, and traits were chosen based on their association with competitive ability, as identified by prior studies. Days to germination is a measure of a seedling's ability to benefit from priority effects where species that establish earlier in the growing season should benefit by sequestering resources first (Sale 1977; Wainwright et al. 2012). Seed mass influences the initial size of the seedling and on seedling provisioning. Consequently, larger seeded species often perform better in competition with other seedlings (Leishman 1999; Turnbull et al. 1999). High water use efficiency can be beneficial to plants facing water stresses but the accompanying decrease in transpiration translates to slowed growth and decreased competitive ability (Drenovsky et al. 2012). Finally, root mass fractions are thought to reflect the differential investment of photosynthates between the aboveground and belowground organs (Titlyanova et al. 1999). For instance, a well-established root can enhance plant recovery from losses of above-ground biomass due to herbivores (Kitajima 1994).

All functional traits were measured on plants grown in the absence of competition. Seed mass and days to germination were measured in pilot trials prior to the experiment. Water-use efficiency was measured as instantaneous gas exchange using a LI-6400 portable gas exchange system (LI-COR, Lincoln, NE, USA). All measures were collected with CO₂ concentration at 400 ppm at an irradiance level of 1500 μmol photons⁻¹. Instantaneous water-use efficiency (WUE) was calculated as the CO₂ assimilation: transpiration ratio. Root mass fraction (RMF) was calculated as root biomass divided by total plant biomass, based on dry weights.

Statistical Analyses

All analyses were conducted in R version 3.2.3 (R Core Team 2015). Each metric for relative interaction intensity (competitive effect or competitive response) was predicted with a linear model where origin and resident species were included as fixed effects, and resident species was nested within origin.

Differences between resident species pools in above-ground biomass, WUE, and RMF were assessed with linear models including origin and resident species nested within origin. A separate analysis also assessed differences in these variables between populations of *B. madritensis* of each origin. Average values for each species were used for days to germination and seed mass because they were collected in a pilot study (supplementary materials), so we used t-tests to determine differences in these traits between the resident species pools from California versus Spain.

To evaluate the relative importance of traits versus fitness of resident species in predicting variation in competitive response and effect of *B. madritensis*, we used a model averaging approach (Grueber et al. 2011). The model averaging approach allows us to consider multiple competing hypotheses simultaneously to identify the best set of models according to Akaike's Information Criterion (AIC), by making inferences based on weighted support from multiple models. In traditional multiple regression approaches there are often step-wise approaches used to identify the best model, but this approach is problematic when there is nearly equivalent support for several different models. Using a top model set derived from model averaging as opposed to a single best model can provide a more robust means of obtaining parameter estimates and making predictions, because it can account for model uncertainty (Burnham and Anderson 2003). Separate analyses were constructed for Spain versus California, to explicitly evaluate our hypothesis that fitness effects would be stronger relative to trait differences in the invaded range of *B. madritensis*. The data set used includes five input variables: (i) seed mass, (ii) days to germination, (iii) root mass fraction (RMF), (iv) Water-use efficiency (WUE) and (v) biomass of competitor (fitness).

To generate a sub-model set, we first fit a global general linear model (GGLM, (Bates et al. 2012)) containing all six variables. Then we standardized the input variables so that the parameter estimates can be interpreted after model averaging (Gelman 2008). Next, we used the dredge function in the *MuMIn* package to consider all combinations of the global model. The dredge function considers all possible combinations of the variables for models. We used `get.models` to select for a subset of those models with an $AIC < 4$. (Grueber et al. 2011). Finally, we performed model averaging on our top submodels ($AIC < 4$). We report the conditional estimate results as they are predictions for a factor of interest at the mean of all other parameters (Grueber et al. 2011). We also report relative importance of each variable which can be derived by summing the Akaike weights across all the models in the sets where that variable occurs (Burnham and Anderson 2003).

RESULTS

Trait and fitness differences

The invasive population of *B. madritensis* had higher individual fitness (above-ground biomass) than the native population, when grown under common greenhouse conditions. Specifically, above-ground biomass of *B. madritensis* individuals from Spain was over four times smaller than for individuals from California (Figure 1: $F_{1,13}=12.64$, $p=0.0035$). When one very high value from California was excluded, the result was still highly significant (Figure 1, Table 2: $F_{1,12}=29.37$ $p<0.001$). Only one other trait differed between the two populations: RMF was higher for *B. madritensis* from Spain when compared to California (Table 2: $F_{1,13}=41.78$, $p<0.001$). Days to germination was determined by recording days until first germinant for each species. Both populations had similar times to germination in our pilot trial and hence no further analysis was performed (mean values in Table 1).

In our analysis comparing the traits of competing species pools, no measured traits differed significantly between the pool of competitor species from California versus Spain (statistical output in Table 2, mean values for each species given in Online Resource 1).

Competitive effect of *B. madritensis* on resident species

Consistent with the predictions of EICA, *B. madritensis* exerted a greater competitive effect on resident species from California than Spain (Origin: $F_{1,97}=14.84$, $p<0.001$, Figure 2, Table 3), but there was considerable variation in the strength of the competitive effect on resident species (Species: $F_{13,97}=6.96$, $p<0.001$).

Competitive response of *B. madritensis* to resident species

Contrary to our initial expectations, *B. madritensis* had a greater reduction in biomass when grown with resident California species (about 40%) compared to when grown with residents of its native Spanish range, (25% biomass reduction; Origin: $F_{1,103}=30.6$, $p<0.0001$, Figure 3a, Table 3). The biomass response of *B. madritensis* to competition again varied depending on the identity of the resident species (Origin(Species): $F_{13,103}=1.81$, $p=0.052$, Figure 3b, Table 3).

Predicting the strength of competition on the basis of trait and fitness differences

We used model averaging to evaluate the relative importance of traits versus fitness of resident species in predicting variation in competitive response and effect of *B. madritensis*. *B. madritensis* from Spain exerted the strongest competitive effect on resident species from Spain with late germination, higher root mass fraction, low water use efficiency and small seeds ($p<0.0001$ and importance = 1.00 for all of these traits, Table 4). *B. madritensis* from California exerted the strongest competitive effect on competitor species with late germination and small seeds (for these traits $p<0.0001$, importance = 1.00, Table 4).

None of the selected traits predicted competitive responses of *B. madritensis* to growth with resident species from Spain (Table 5). *B. madritensis* collected in California had the greatest response to competition (reduction in biomass) when competing with resident species that had earlier germination times ($p=0.038$, weighted importance = 0.81, Table 5).

Fitness (above-ground biomass of the competitor) was not a significant predictor of variation in the strength of competitive effect or response of *B. madritensis*.

DISCUSSION

A major goal of invasion biology is to conduct robust tests of niche-based theories of community assembly, such as the theory of limiting similarity or the EICA hypothesis. While many of our findings were consistent with the predictions of these theories, others were surprising. For instance, *B. madritensis* individuals grown from seeds collected from its invasive range in California grew significantly larger (had higher above-ground biomass) than individuals from seeds collected in the native range in Spain (consistent with EICA). Also consistent with EICA, *B. madritensis* from Spain allocated a smaller proportion of biomass above-ground than individuals from California. Competitive interactions were also stronger between *B. madritensis* and resident species from California; *B. madritensis* had a greater competitive effect on resident species from Californian (consistent with predictions of EICA) as well as a greater competitive response to those species (unexpected based on EICA predictions). Consistent with niche-based theories of community assembly, variation in the competitive effect and response of *B. madritensis* could be predicted by functional traits of the resident competitor species. However, traits were less important for predicting the competitive response than competitive effect of *B. madritensis*, especially for the population of Spanish origin. Fitness did not appear in any model suggesting that the role of fitness in predicting competitive outcomes may be overstated. These findings are discussed in detail below.

Our results show that the invasive population of *B. madritensis* in California achieved larger sizes and allocated a lower proportion of biomass to roots than individuals from its native range, a finding consistent with the EICA hypothesis. For instance, a recent meta-analysis found populations of invasive species were on-average larger, more abundant and had higher reproductive output in their invasive range, although there was significant variation in these responses (Parker et al. 2013). Several studies have shown that competitive advantages of invasive species are associated with changes in biomass allocation, not just individual size (Meyer and Hull-Sanders 2008; Morrison and Mauck 2007; Pattison et al. 1998; Wilsey and Polley 2006). In our study, the decreased biomass allocation to roots

in invasive population of *B. madritensis* may be associated with adaptations to higher soil resource levels or increased light competition in the invasive range (Iwasa and Roughgarden 1984; Poorter et al. 2012).

The differences in size and traits of *B. madritensis* populations likely contributed to the variation in competitive interactions we observed. Notably, competitive interactions were stronger between *B. madritensis* and resident species from its invaded range; the biomass of both *B. madritensis* and its competitors from California were reduced by twice as much when grown together than biomass reductions observed for the Spanish communities. These competitive effect results support our hypothesis that *B. madritensis* should exert stronger competitive effects on species in its invaded than native range. Our findings also support past studies showing that competitive effects of invasive species on species in their introduced ranges are generally stronger than on those in their native ranges (Ni et al. 2010; Vila and Weiner 2004). In contrast, our finding that *B. madritensis* was more competitively suppressed by residents in California than Spain (as measured by resident competitor species abilities to suppress its growth) was unexpected, and potentially suggests that community assembly processes in Californian communities select for species and genotypes with strong competitive abilities. These results support the conclusion that the invasion of *B. madritensis* into California is not due to weaker competitive resistance of the California resident communities than are found in Spain. It is worth noting, however, that studies of other invaders have come to the opposite conclusions, (see for example Callaway et al. 2011) suggesting that biogeographic variation in competition intensity can vary by system and species.

While we originally hypothesized that both traits and fitness would contribute to invader success of *B. madritensis*, fitness was noticeably absent from predictors of competitive effect and responses in both ranges. Despite the large difference in biomass between native and introduced populations of *B. madritensis*, no models included fitness of resident competitors as a significant predictor of competitive outcomes, suggesting that community assembly in this system is more strongly mediated by traits than fitness differences among competing species. Our results are consistent with prior studies predicting that species traits can predict the impact of invasions (MacDougall et al. 2009; Pyšek et al. 2012), and that trait-derived competitive hierarchies are better predictors of competitive interactions than size-based fitness hierarchies (Kraft et al. 2014; Kunstler et al. 2012) even in invaded systems (Lai et al. 2015). To our knowledge, however, this is the first example of a trait-based competitive hierarchy in the competitive interactions of species in their native versus invaded ranges, uniquely allowing us to draw conclusions about the specific traits likely to predict invasion success in this system.

Our experiment showed that both competitive effects and responses of *B. madritensis* were predicted by traits, but those traits differed between the invaded and native ranges. Further, although competitive effect and response were both stronger in California, we found variation in the suite of traits predictive of competitive effect versus response, as was initially predicted by Goldberg (1990). Only one trait was predictive of the competitive response of *B. madritensis*, and only in California. Early germination was the best predictor of a negative competitive response of *B. madritensis* to being grown in competition with resident species from California, a result consistent with restoration experiments showing that areas seeded with early germinating native species had the lowest rates of invasion by early-germinating exotic species such as *B. madritensis* (Cleland et al. 2013). In contrast, multiple traits predicted the competitive effect of *B. madritensis* on resident species. *B. madritensis* had the greatest competitive effect on species with late germination and small seeds, in both California and Spain. Species that germinate later in the growing season can be competitively suppressed by earlier active species that can pre-empt space and resources (Wainwright et al. 2012), and smaller seeded species have lower provisioning to support initial life stages. This suggests that native species with these traits are most likely to be negatively impacted by highly competitive invading species, and offers a potential way for land managers to predict native species that might be important conservation priorities in areas at risk of invasion.

In Spain, species with low water use efficiency and high allocation to roots were also more negatively impacted by competition with *B. madritensis*. It is interesting to note that traits had greater predictive power to explain variation in the competitive effect of *B. madritensis* in its native versus invasive range, and potentially suggests a greater signal of trait-based community assembly in that system. In highly invaded areas such as Southern California, multiple invasions could alter environmental niche space and cause a kind of "disassembly" process (Reynolds et al.

2017), weakening the signal of trait-based community assembly. Further, these results highlight that the traits predicting competitive effect and response can differ in key ways that deserve future investigation.

As with any experiment ours has some important caveats. First, competitor biomass in this study was defined by above-ground biomass, and differences we observed in root allocation of *B. madritensis* between its native and invaded ranges suggests that root competition could be important for understanding its success as an invader. Second, our resident pools included both native and naturalized non-native species. While maximizes the realism of our results, in quantifying competitive interactions with representative species pools, our results need to be interpreted carefully, as they do not strictly quantify variation in interactions between native and non-native species. Similarly, in this study we focused on competitive effect and response of our focal invader, *B. madritensis*. However, we did not focus on competitive effect and response of the resident species; studies on the competitive effects and responses of residents would be ideal for identifying species to plant in restorations, that are minimally effected by competition from invasive species. Finally, our competitive species pool included both annual and perennial species, but our experiment was limited to the first growing season following germination. However, competition between an annual species like *B. madritensis* and a perennial species can change over time. Another study in California showed that that native perennial species are competitively suppressed as seedlings by annual invading species, but in later years the relationship flips, and perennial species can competitively suppress annuals (Goldstein & Suding 2014).

In conclusion, this study aimed to determine the relative roles of functional traits and fitness differences for predicting both the response of an invader to competition with residents, and the competitive effect of the invader on residents. Overall, these results indicate that competitive interactions of *B. madritensis* in its native and invaded ranges are driven by functional traits rather than fitness differences although there may be other factors at play environmentally since fitness did not appear in any of our models. We propose that trait based community assembly processes are likely to vary in strength with biogeography. This study shows that different suites of traits may aid in identifying those native species likely to strongly compete with invaders, versus those than will be competitively suppressed by invaders, with important implications for invasion control efforts by land managers. We suggest that future competition experiments consider the context dependent nature of the effect of different traits on competition as it relates to invasions.

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Fig. 1 Above-ground biomass of *B. madritensis* individuals (in grams) from seeds collected in the native range (Spain) and invasive range (California), grown with and without interspecific competition. Error bars indicate 1 +/- SE of the mean

Fig. 2 a Competitive effect of each population *B. madritensis* (as measured by the proportional decrease in the biomass of a competitor species when in the presence of *B. madritensis*, RII) when grown with each *B. madritensis* population: from California (grey bars) or Spain (white bars). **b** Average value of *B. madritensis*' competitive effect on all species in each place of origin. Error bars indicate 1 +/- SE of the mean

Fig. 3 a Competitive response of each population *B. madritensis* (as measured by the proportional decrease in its biomass in the presence of a competitor species, RII) when grown with each competitor species from California (grey bars) or Spain (white bars). **b** Average value of *B. madritensis*' competitive response to all species in each place of origin. Error bars indicate 1 +/- SE of the mean

Fig. 4 a Root mass fraction (RMF) of each population of *B. madritensis* and competitor species from each place of origin: from California (grey bars) or Spain (white bars). **b** Average RMF for all species in each place of origin. Error bars indicate 1 +/- SE of the mean

1 TABLES

2

3 **Table 1** Competitor species and target species utilized in the experiment, including the abbreviation used in figures, common name, functional group and mean
 4 functional traits. AG=above ground. Target species highlighted in bold
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Scientific name	Abbrv	Origin	Common name	Functional group	AG Biomass (g)	Root mass Fraction (g)	Seed mass (g)	Days to germination	Water use efficiency ($\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$)
<i>Avena barbata</i>	AVBA	Spain	Slender Wild Oat	Annual grass	0.0088	0.8	0.0059	7	2218
<i>Plantago lagopus</i>	PLLA	Spain	Canary grass	Annual forb	0.0029	0.55	0.00028	16	1470
<i>Bromus tectorum</i>	BRTE	Spain	Drooping Brome	Annual grass	0.0029	0.84	0.0024	6	7519
<i>Hypochoeris glabra</i>	HYGL	Spain	Smooth Cat's ear	Annual forb	0.0015	0.51	0.0006	6	1471
<i>Trifolium cherleri</i>	TRCH	Spain	Cupped Clover	Annual forb	0.015	0.53	0.0012	8	2292
<i>Leontodon taraxacoides</i>	LETA	Spain	Lesser hawkbit	Annual forb	0.0039	0.56	0.00037	4	896
<i>Bromus hordeaceus</i>	BRHO	Spain	Soft brome	Annual grass	0.0017	0.89	0.0014	8	9044
<i>Rumex crispus</i> *	RUCR	California	Curly Dock	Perennial forb	0.008	0.58	0.0037	11	2481
<i>Lasthenia californica</i>	LACA	California	California goldfields	Annual forb	0.0015	0.62	0.0016	20	939
<i>Festuca myuros</i> *	FEMY	California	Rat-tail fescue	Annual grass	0.0059	0.63	0.00086	6	20538
<i>Festuca microstachys</i>	FEMI	California	Pacific Fescue	Annual grass	0.003	0.78	0.0015	5	3704
<i>Clarkia purpurea</i>	CLPU	California	Winecup Clarkia	Annual grass	0.0049	0.44	0.00035	16	3995
<i>Festuca rubra</i>	FERU	California	Red Fescue	Annual grass	0.0052	0.79	0.0011	6	4444
<i>Eschscholzia californica</i>	ESCA	California	California Poppy	Perennial forb	0.0036	0.47	0.00018	6	2961
<i>Festuca perennis</i> *	FEPE	California	Wild rye	Annual grass	0.014	0.72	0.0047	6	6599
<i>Bromus madritensis</i>	BRMA	California	Compact brome	Annual grass	0.0086	0.62	0.0017	8	2937
<i>Bromus madritensis</i>	BRMA	Spain	Compact brome	Annual grass	0.002	0.89	0.0018	8	7883

6 *Listed in the Invasive Plant Inventory for California according to the California Invasive Plant Council. All species are naturalized in California and but with
 7 different invasion ratings: *R. crispus* - limited concern, *F. myuros* - moderate concern, and *F. perennis* - moderate concern.

8 **Table 2.** Functional trait differences between *B. madritensis* (BRMA) collected in California (CA) versus Spain
9 (ES) and between the suites of resident competitor species chosen from California versus Spain. All values were
10 measured on plants grown in the absence of competition. A separate analysis was performed for each trait. Mean
11 values for seed mass and days to germination were used, based on pilot analyses (measures were not taken on
12 individuals in the experiment). Variation in denominator degrees of freedom (df2) for analyses of *B. madritensis*
13 traits reflect removal of outliers (see Methods). Significant terms highlighted in bold.

Species	Trait	CA mean	ES mean	Std. Error	(df1, df2)	F value	P value
BRMA	Water-use efficiency	2937	4887	1162	1,11	2.82	0.12
	Root mass fraction	0.62	0.88	0.04	1,13	41.8	<0.001
	Above-ground biomass (g)	0.007	0.002	9.2e-4	1,12	29.4	<0.001
	Seed mass (g)	0.0017	0.0018	3.2e-4	1,8	0.68	0.43
Competitors	Water-use efficiency	4439.1	4181.3	948	1,92	1.07	0.79
	Root mass fraction	0.64	0.69	0.04	1,92	1.17	0.28
	Seed mass (g)	0.002	0.0019	3.7e-4	1,92	0.16	0.69
	Above-ground biomass (g)	0.006	0.004	1.3e-3	1,92	0.81	0.37
	Days to germination	9.21	7.71	0.85	1,92	1.91	0.17

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42 **Table 3** Effects of origin and resident competitor species identity (nested within Origin) on competitive response
 43 and competitive effect of *B. madritensis*. Significant terms highlighted in bold.

	Variables	(df1, df2)	F value	P value
Competitive response	Origin	1,103	30.6	<0.001
	Origin(Species)	13,103	1.81	0.052
Competitive effect	Origin	1,97	14.9	<0.001
	Origin(Species)	13,97	6.97	<0.001

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80 **Table 4.** The relative importance of resident competitor functional traits for predicting the competitive effect of *B.*
 81 *madritensis* on resident species from Spain or California. Fitness in this model is represented by competitor above-
 82 ground biomass (Comp biomass). SE=Adjusted standard error from the model output. Significant terms highlighted
 83 in bold.
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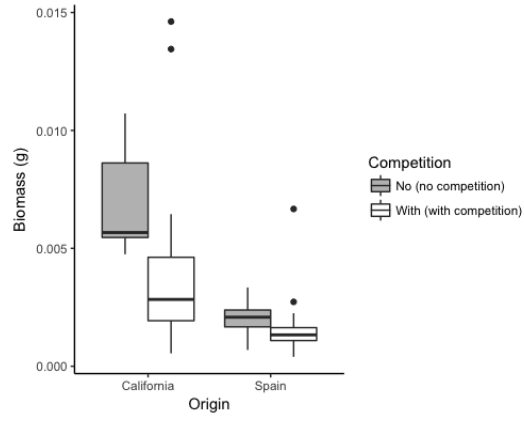
Origin	Parameter	Estimate	SE	z-value	p-value	Relative Importance
Spain	(Intercept)	1.7e+00	1.3e-01	12.79	< 0.001	
	Root mass fraction	-4.0e+00	2.8e-01	14.59	<0.001	1.00
	Water use efficiency	1.6e-04	1.2e-05	14.08	<0.001	1.00
	Seed mass	2.0e+02	1.3e+01	16.07	< 0.001	1.00
	Days to germination	-1.7e-02	3.0e-03	5.72	< 0.001	1.00
California	Comp biomass	-2.1e+00	3.7e+00	0.57	0.57	0.29
	(Intercept)	-2.8e-01	5.7e-02	4.95	<0.001	
	Root mass fraction	9.6e-03	1.2e-01	0.08	0.93	0.24
	Water use efficiency	-3.8e-06	2.1e-06	1.84	0.07	0.69
	Seed mass	2.0e+01	7.7e+00	2.67	0.007	1.00
	Days to germination	-1.4e-02	2.8e-03	5.06	<0.001	1.00
	Comp biomass	8.0e-01	8.8e-01	0.91	0.36	0.33

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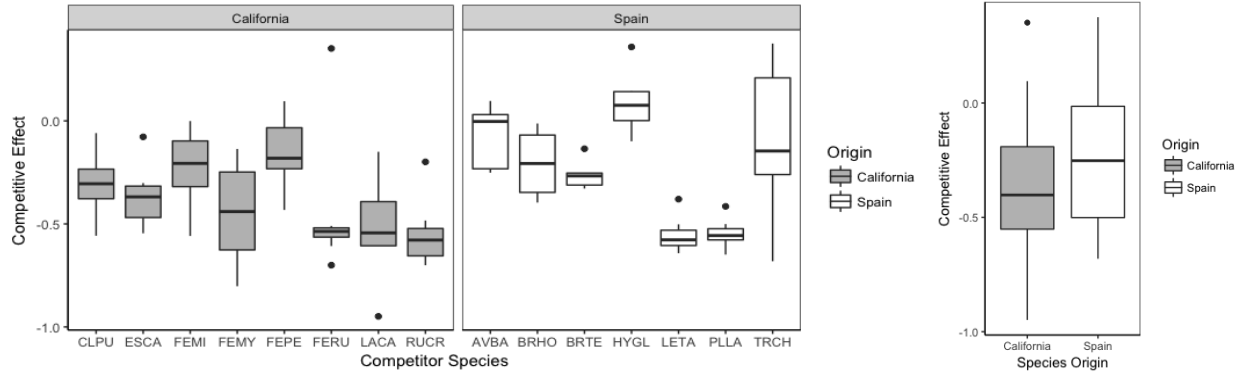
110 **Table 5.** The relative importance of resident competitor functional traits for predicting the competitive response of
 111 *B. madritensis* to being grown with resident species from Spain or California. Fitness in this model is represented by
 112 competitor above-ground biomass (Comp biomass). SE=Adjusted standard error from the model output. Significant
 113 terms highlighted in bold

Origin	Parameter	Estimate	SE	z value	Pr(> z)	Relative Importance
Spain	(Intercept)	6.0e-02	3.6e-01	0.17	0.87	
	Root mass fraction	8.1e-01	1.0e+00	0.80	0.42	0.45
	Water use efficiency	-3.9e-05	3.6e-05	1.07	0.29	0.57
	Seed mass	-4.6e+01	4.2e+01	1.11	0.27	0.48
	Days to germination	2.7e-03	7.2e-03	0.38	0.71	0.20
	Comp biomass	9.5e-01	1.7e+00	0.55	0.58	0.25
California	(Intercept)	-5.3e-01	2.3e-01	2.33	0.02	
	Root mass fraction	-2.1e-01	4.2e-01	0.50	0.61	0.23
	Water use efficiency	1.3e-05	8.1e-06	1.58	0.11	0.49
	Seed mass	-3.2e+01	3.1e+01	1.05	0.30	0.33
	Days to germination	2.1e-02	1.0e-02	2.08	0.038	0.81
	Comp biomass	-5.7e+00	4.3e+00	1.32	0.19	0.44

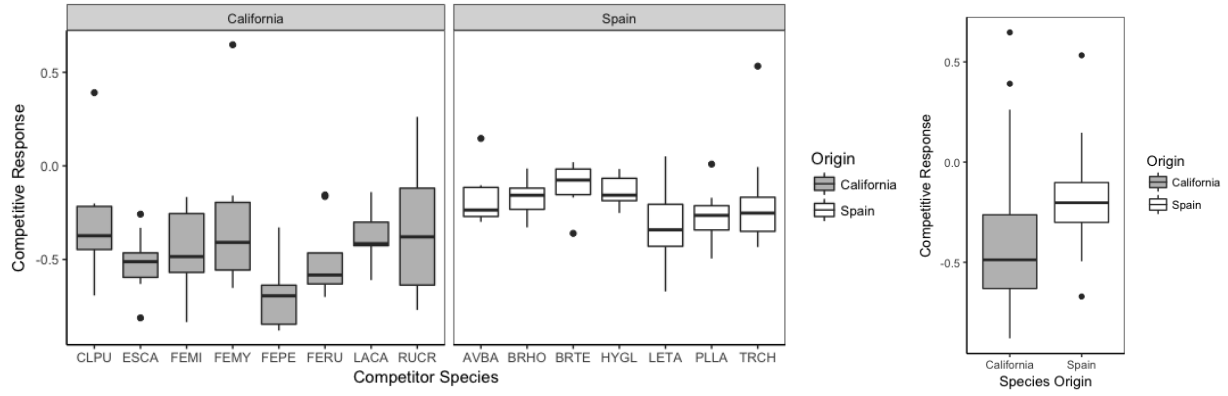
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